From individual heterogeneity to population-level overdispersion: quantifying the relative roles of host exposure and parasite establishment in driving aggregated helminth distributions

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ABSTRACT

In most host-parasite systems, variation in parasite burden among hosts drives transmission dynamics. Heavily infected individuals introduce disproportionate numbers of infective stages into host populations or surrounding environments, causing sharp increases in frequency of infection. Parasite aggregation within host populations may result from variation among hosts in exposure to infective propagules and probability of subsequent establishment of parasites in the host. This is because individual host heterogeneities contribute to a pattern of parasite overdispersion that emerges at the population level. We quantified relative roles of host exposure and parasite establishment in producing variation in parasite burdens, to predict which hosts are more likely to bear heavy burdens, using big brown bats (*Eptesicus fuscus*) and their helminths as a model system. We captured bats from seven colonies in Michigan and Indiana, USA, assessed their helminth burdens, and collected data on intrinsic and extrinsic variables related to exposure, establishment, or both. Digenetic trematodes had the highest prevalence and mean abundance while cestodes and nematodes had much lower prevalence and mean abundance. Structural equation modeling revealed that best-fitting models to explain variations in parasite burden included genetic heterozygosity and immunocompetence as well as distance to the nearest water source and the year of host capture. Thus, both differential host exposure and differential parasite establishment significantly influence heterogeneous helminth burdens, thus driving population-level patterns of parasite aggregation.

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1. Introduction

Variation in parasite burden among hosts is a key feature in transmission dynamics in most parasitic species (Anderson and May, 1982, 1985a,b). Parasites are usually aggregated, or overdispersed, in a host population and a minority of individuals bears the bulk of the parasitic burden, while most individuals have few or no parasites (Crofton, 1971; Wakelin, 1985; Shaw and Dobson, 1995; Shaw et al., 1998; Galvani, 2003; Poulin, 2004, 2007, 2011; Craig et al., 2007; Marques et al., 2010). More heavily infected individuals introduce a disproportionate number of infective propagules into the host population, thus maintaining a pathogen's basic reproductive ratio (Anderson et al., 1991; McCallum et al., 2001). These host individuals may act as super-spreaders (cf. Lloyd-Smith et al., 2005) by disproportionately infecting other individuals in the population, leading to sharp increases in the frequency of infection within a population (Fujie and Odagaki, 2007; Paull et al., 2012).

Heterogeneity among individuals in infection risk and parasite load is the outcome of variation in both host exposure and subsequent parasite establishment within hosts (i.e., host susceptibility; Poulin, 2011). This individual level heterogeneity, both inside the host and in the host's environment, provides a mechanism behind patterns of parasite aggregation that then emerge at the population level. Although classic transmission models ignore this distinction between the processes of exposure and establishment (McCallum et al., 2001; Beldomenico and Begon, 2010), separating them can improve predictions of disease dynamics and highlight the fundamental drivers of parasite transmission (e.g., Civitello and Rohr, 2014; Roche et al., 2015). Models that have incorporated host heterogeneity in factors such as host size and coinfection reliably predicted levels of parasite aggregation in field data from

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an amphibian—trematode system (Wilber et al., 2017). In addition, models that incorporate host condition-linked immunity regularly predict aggregation of infective stages (Morrill and Forbes, 2012, 2016). Based on empirical data, intrinsic variation among hosts in behavior, immunity, physiological condition, and genotype can all influence the probabilities of both exposure and subsequent establishment (e.g., Perkins et al., 2008; Hawley et al., 2005; Hoye et al., 2012; Voegeli et al., 2012; Cornet et al., 2014; Warburton et al., 2016a), and experimental manipulations of host heterogeneity, by limiting anti-parasite behaviors or changing how hosts interact with their environment, have been shown to significantly impact the degree of parasite aggregation (Bandilla et al., 2005; Johnson and Hoverman, 2014). At the same time, variation in extrinsic factors such as temperature, precipitation, and the distribution and abundance of habitats, may affect pathogen survival or population dynamics and result in spatial or temporal variation in the distribution of infective propagules and/or infected vectors or hosts (e.g., Keymer and Anderson, 1979; Bohan, 2000; Hansen et al., 2004; Warburton et al., 2016b). This may lead to heterogeneities among hosts in the probability of encountering infective propagules (Brunner and Ostfeld, 2008; Paull et al., 2012) and result in landscapes characterized by spatially variable infection risk and transmission dynamics (Meentemeyer et al., 2012). Although the specific mechanisms driving aggregation might not be universal across all host-parasite systems (see Poulin, 2013), host heterogeneity in parasite exposure or host susceptibility is likely to be an important driver of patterns of parasite burden among hosts in natural populations.

To fully understand population level patterns in parasite burdens and the eco-evolutionary dynamics of host-parasite interactions, we need to characterize the suite of intrinsic and extrinsic factors that interact to produce individual variation in both host exposure and susceptibility that drives parasite burdens at the level of the individual host. Theoretical evidence suggests that even if the probability of encountering parasites is random, differences among hosts in resistance potential are sufficient to result in parasite aggregation among hosts (Morrill and Forbes, 2012), and there is some empirical evidence that indicates that host factors such as body size and genetic diversity may outweigh the importance of extrinsic (environmental) factors in determining parasite burdens (e.g., Cardon et al., 2011). Conversely, there is also experimental and empirical evidence indicating that extrinsic factors may be more important than host factors (Karvonen et al., 2004; Bandilla et al., 2005; Calabrese et al., 2011) or that both may be important (e.g., Stanko et al., 2015; Young et al., 2015). In general, few studies have simultaneously examined a wide range of intrinsic and extrinsic variables, yet such data are crucial for populating models of disease transmission and for the design of effective control programs (Woolhouse et al., 1997).

Here we utilize a multi-year, multi-region set of predictive variables to identify extrinsic and intrinsic variables associated with increased helminth burdens in the big brown bat, *Eptesicus fuscus* (Chiroptera: Vespertilionidae). We collected data on a wide variety of extrinsic (site, availability of aquatic habitats, dominant land use, and month and year of capture) and intrinsic (sex, age, body condition, immune function, genetic diversity) variables that may influence either exposure or establishment and used a causal modeling approach (structural equation modeling) to examine their relative role in determining the number of parasites per host. Unlike traditional regression models, this approach allowed us to model latent, unobservable variables by building indices from observed variables (Shipley, 2000). This method is particularly useful for analyzing direct and indirect effects of many variables within large population data sets (Grace et al., 2010). Quantifying the mechanisms that produced variation in helminth burdens allowed us to identify the key factors that influence individual

parasite loads, thus identifying hosts that contribute to population level patterns of parasite aggregation and that may have an outsized influence on parasite transmission dynamics.

2. Materials and methods

2.1. Host—parasite system

The big brown bat is a large (15–24 g) insectivorous bat species and is one of the most common bats found throughout temperate North America. Females aggregate in buildings or trees during the summer while males may be found in the same roosts as females or may roost solitarily (Kurta and Baker, 1990). Colony members typically forage for insects within the vicinity of the roost site (Kurta and Baker, 1990); however, bats have been observed foraging up to 11–13 km from their roost (Wilkinson and Barclay, 1997; Arbuthnott and Brigham, 2007). During pregnancy and lactation, female bats will forage heavily throughout the night as they require much more energy during this period (Kurta et al., 1990). Conversely, males and non-reproductive females will often forage for much shorter periods, usually for 1–2 h after sunset (Kurta, 1995; Altringham, 1996; Neuweiler, 2000). Big brown bats typically become infected with helminths after ingesting an arthropod acting as an intermediate host, although some bat nematodes such as *Litomosoides* spp. are blood-borne and vectored by hematophagous arthropods (Esslinger, 1973). Most of these helminths are digenetic trematodes (Platyhelminthes: Trematoda) with a lifecycle that includes three hosts. Two of these hosts are aquatic: snails act as a first intermediate host while insects with aquatic stages act as a second intermediate host (Schell, 1985, Kumar, 1999). The cestodes such as *Hymenolepis* spp. and some nematodes such as *Rictularia* spp. are acquired via ingestion of a terrestrial beetle acting as an intermediate host (Rausch, 1975; Esteban et al., 2001). During a given night bats may forage over multiple habitats (e.g. forests, grasslands, urban areas, agricultural fields, and over water or wetlands), and not all individuals sharing a roost will forage in the same locations (e.g. Wilkinson and Barclay, 1997). Further, the exact mix of different habitats available to forage in varies considerably from roost to roost and big brown bats are known to forage over a wide diversity of habitats (e.g. Lookingbill et al., 2010). Therefore, within and between localities hosts may vary in the number, identity, and diversity of insects they encounter and eat, and hence the number of infective propagules to which they are exposed.

2.2. Host capture and helminth collection

Four hundred and twenty-two *E. fuscus* (55% female, 45% male and 64% adult, 36% juvenile) were captured from 16 sites in the midwestern USA (Michigan, Indiana, and Kentucky, Fig. 1) with mist nets as they emerged from their roosts or were hand-caught in the roost prior to nightly emergence. Bats captured in the same roost were considered to belong to the same site. The majority of sites in Michigan (2 through 6) were sampled a single time in 2008 (Supplementary Table S1). Most sites were subsequently sampled twice per year for 2 years (2009–2010) with the exceptions of 1 and 15 which were sampled a single time only in 2009 because bats were excluded from their roosts by homeowners after initial sampling. The first time point depended on weather that was warm enough to allow bats to reliably rouse from torpor at night (early to mid-May). The second time point (late July/early August) needed to occur after young bats became volant but before adults began to store body fat for winter torpor. No bats were captured while females were gestating and no obviously pregnant bat was necropsied. Host sex, host age based on the ossification of